

RODENTS OF THE FAMILY ANOMALURIDAE (MAMMALIA)  
FROM SOUTHEAST ASIA (MIDDLE EOCENE,  
PONDAUNG FORMATION, MYANMAR)

MARY R. DAWSON

Curator, Section of Vertebrate Paleontology

TAKEHISA TSUBAMOTO<sup>1</sup>

MASANARU TAKAI<sup>1</sup>

NAOKO EGI<sup>1</sup>

SOE THURA TUN<sup>2</sup>

CHIT SEIN<sup>2</sup>

ABSTRACT

Latest middle Eocene deposits in the Pondaung Formation of Myanmar have yielded specimens representing the rodent family Anomaluridae. This is the geologically oldest record of the family. There appear to be two or three species of Pondaung anomalurids, the most completely represented taxon of which is described as a new genus and species, *Pondaungimys anomaluropis*. The anomalurids from the Pondaung Formation are characterized by a complex folding pattern on the occlusal surfaces of the cheek teeth, as well as the basically anomalurid pentalophodont condition. Undescribed anomalurids have been reported from the late Eocene of Thailand and Oligocene of Pakistan and the Arabian Peninsula. Their Neogene distribution is only African. This occurrence in the Pondaung Formation adds new evidence to previously reported similarities between Southeast Asian and North African Paleogene mammalian faunas.

KEY WORDS: Rodentia, Anomaluridae, *Pondaungimys*, Middle Eocene, Myanmar

INTRODUCTION

The richly fossiliferous Pondaung Formation of Myanmar has long been known for its record of middle Eocene terrestrial mammals (Pilgrim and Cotter, 1916; Tsubamoto et al., 2000, 2002), including a diversity of Primates, Perissodactyla, and Artiodactyla. Along with the more recently discovered late Eocene fauna from the Krabi Basin of Thailand (Chaimanee et al., 1997; Ducrocq et al., 1997), the Pondaung fauna provides an important record of Paleogene evolutionary and paleogeographic events in southeastern Asia. Increasingly, these faunas show some interesting similarities with others from the Paleogene of northern Africa (Ducrocq et al., 2000).

Recently field teams from Kyoto University and the Myanmar Government have discovered the rodent specimens that are the subject of this report. While rodents have been mentioned in faunal lists from the Pondaung Formation, previously these specimens were not examined in detail and were given only a questionable familial assignment of

<sup>1</sup> Primate Research Institute, Kyoto University, Inuyama, Aichi 484-8506, Japan.

<sup>2</sup> Department of Geology, University of Yangon, Yangon, Myanmar.

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Phiomysidae indet. (Tsubamoto et al., 2000). They provide evidence for an additional instance of faunal affinities between Southeast Asian and African faunas, representing as they do two or three species referable to the family Anomaluridae, a family that has been endemic to Africa throughout the Neogene. The three extant genera of anomalurids, *Anomalurus*, *Zenkerella*, and *Idiurus*, live in central and western Africa.

The Paleogene fossil record of the anomalurids is sparse. The first to be described, and previously geologically oldest, was *Nementchamys lavocati* from the late middle or late Eocene Bir El Ater (or Nementcha) locality of Algeria (Jaeger et al., 1985). Other reports of anomalurids from the Paleogene of Asia include recognition of the family in the Krabi mine of Thailand, 40 meters above the main lignite seam (Ducrocq et al., 1997) and in the Oligocene of Oman (Thomas et al., 1999). In Baluchistan, anomalurids have been reported from the Oligocene of the Bugti Hills (Welcomme et al., 2001). Presence of a fragment of an anomalurid bone in the upper levels of the Fayum has been mentioned (Lavocat, 1973), although this occurrence has not been authenticated by a description.

### *Terminology and Abbreviations*

Dental terminology follows Jaeger et al., 1985.

NMMP: National Museum, Myanmar, Paleontology.

KU: Kyoto University of Japan.

### *Geologic Setting*

The Pondaung Formation is distributed in the western part of central Myanmar (Fig. 1). It overlies and partially interfingers with the Tabyin Formation and is conformably overlain by the Yaw Formation (Stamp, 1922; Bender, 1983; Aye Ko Aung, 1999). The Tabyin Formation consists mainly of marine claystones, yielding *Nummulites acutus*, a benthic foraminifera indicative of the middle Eocene (Eames, 1951; Bender, 1983); whereas the Yaw Formation is mainly composed of marine shales and yields benthic foraminifera (e.g., *Nummulites yawensis*, *Discocyclina sella*, and *Operculina* sp. cf. *O. canalifera*) and molluscs (e.g., *Velates perversus*), both of which indicate the late Eocene (Bender, 1983).

The Pondaung Formation was re-defined as the freshwater deposits of the Pondaung Sandstones (Cotter, 1914) by Aye Ko Aung (1999). The Pondaung Formation (about 2000 m in thickness) consists of alternating mudstone, sandstone, and conglomerate, and is subdivided into the "Lower" and "Upper" Members (Aye Ko Aung, 1999). The "Lower Member" (about 1500 m in thickness) is dominated by greenish pebbly sandstone and mudstone and contains a few fragments of leaf fossils in its upper part (Aye Ko Aung, 1999). The "Upper Member" (about 500 m in thickness) is dominated by fine- to medium-grained sandstone and variegated mudstone (Aye Ko Aung, 1999; Aung Naing Soe, 1999; Aung Naing Soe et al., 2002) and contains many terrestrial mammalian and other vertebrate fossils (e.g., Pilgrim and Cotter, 1916; Pilgrim, 1925, 1927, 1928; Colbert, 1937, 1938; Bender, 1983; Tsubamoto et al., 2000). The mammalian fauna suggests a Bartonian Age (late middle Eocene) for the "Upper Member" (e.g., Holroyd and Ciochon, 1994, 1995). The fission-track age of the "Upper Member" has been calibrated as  $37.2 \pm 1.3$  Ma (= around middle-late Eocene boundary) (Tsubamoto et al., 2002). Therefore, the age of the "Upper Member" is likely to be the latest middle Eocene.

Most mammalian fossils from the Pondaung Formation have been recovered from the lower half of the "Upper Member" (Aye Ko Aung, 2001). The currently known fossil sites for the Pondaung fauna are distributed on the west side of the Chindwin River, extending about 50 km from northwest to southeast, and are roughly divided into three main areas, that is, Bahin, Pangan, and Mogaung (Fig. 1; Tsubamoto et al., 2000).

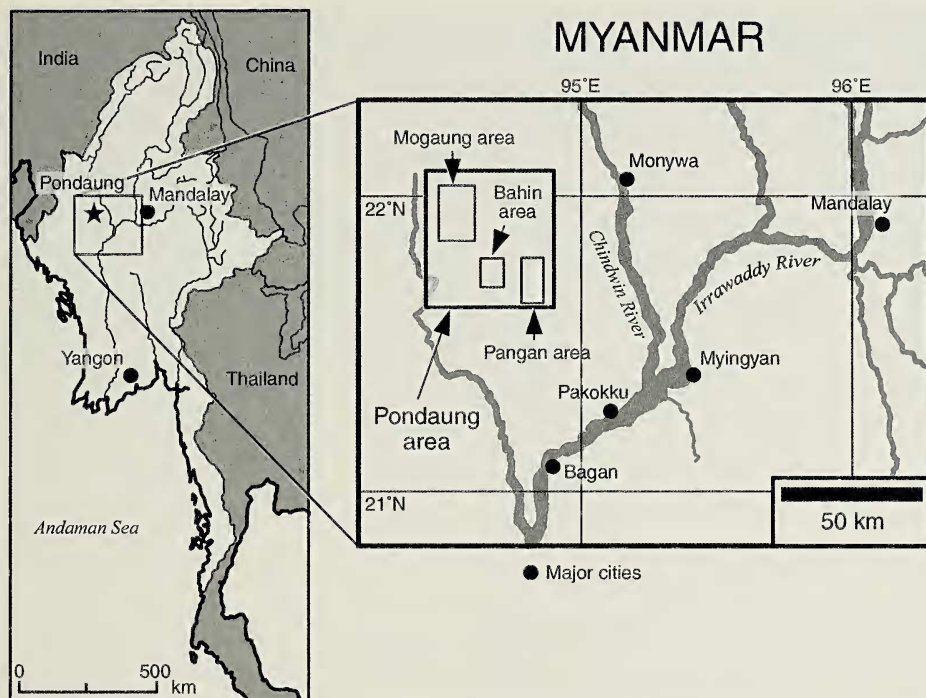


Fig. 1.—Left. Map of part of Southeast Asia showing the location of the Pondaung area within Myanmar. Right. Pondaung area showing localities where the rodent fossils were collected.

#### SYSTEMATIC PALEONTOLOGY

##### Family Anomaluridae

##### *Pondaungimys anomaluopsis*, new genus and species

##### Fig. 2

Synonymy: ?Phiomyidae indet. C in Tsubamoto et al., 2000, p. 38–39, Plate 1, A–C.

*Holotype*.—NMMP-KU 0213, a left mandibular fragment with  $M_{1-3}$ .

*Repository*.—National Museum, Yangon, Myanmar.

*Locality*.—Bh1 locality, Bahin area (Fig. 1; Tsubamoto et al., 2000, fig. 5).

*Formation and Age*.—Lower part of the “Upper Member” of the Pondaung Formation; latest middle Eocene.

*Diagnosis*.—Anomalurid with molars increasing in length from  $M_1$ – $M_3$ , more lophate than cusate; lower molars having elevated cingula around lingual side and pentalophodont occlusal pattern composed of an anterolophid, metalophulid I, mesolophid, hypolophid, and posterolophid. Metalophulid I and mesolophid complexly branching. Compared to *Nementchamys*, *Pondaungimys* has a less well-developed metalophulid I and fewer small complex folds in the trigonid and central basins. Differs from known Neogene anomalurids in having weaker crests in the occlusal pattern and more complex crenulations.

*Dental Measurements*.—See Table 1.



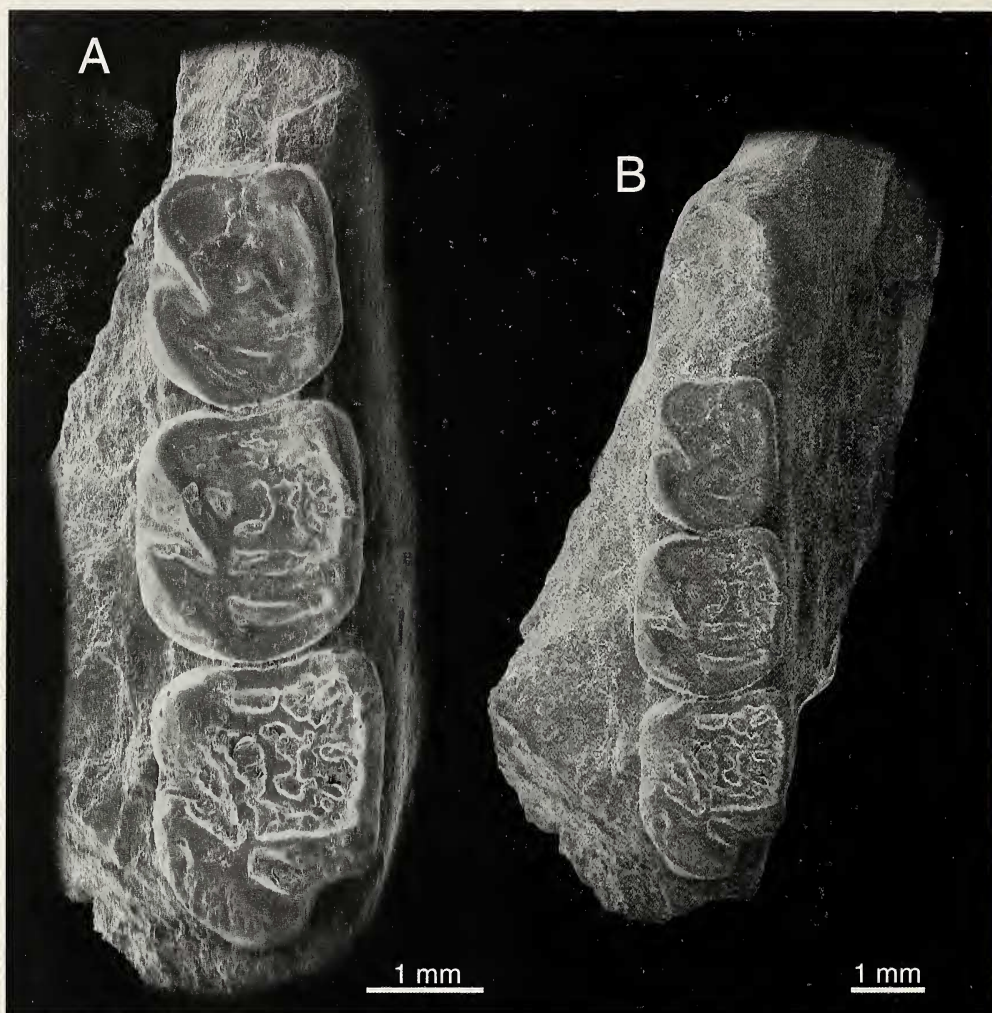


Fig. 2.—*Pondaungimys anomaluropsis*, new genus and species, holotype: NMMP-KU 0213, left mandibular fragment with  $M_{1-3}$ . A. Occlusal view of teeth. B. Entire specimen showing jaw structure.

*Etymology*.—For the genus, Pondaung Formation, and *mys*, Greek, mouse; for the species, Gr. *anomaluros*, different, and *opsis*, like, referring to the familial affinities of this rodent.

*Description*.—An incomplete left mandible with  $M_1$ – $M_3$  and the alveolus of  $P_4$ , NMMP-KU 0213 (Fig. 2), represents a new taxon of anomalurid rodent. The mandible appears to have been sturdily built. At the diastema the mandible drops down only gradually anterior to the alveolus of  $P_4$ . There appears to have been a mental foramen high on the jaw below the diastema just anterior to the alveolus of  $P_4$ . The masseteric fossa is deeply concave and extends forward to below the trigonid of  $M_2$ ; its ventral ridge continues forward to below the middle of  $M_1$ . The mandible differs from that of Recent *Anomalurus* but shares some characters with species of the Miocene *Paranomalurus* (Lavocat, 1973): the lack of a drop of the mandible anterior to  $P_4$  occurs also in *P. soniae*, whereas the distinct masseteric fossa can be found in *P. bishopi*. Unfortunately, the posterior-most part of the mandible, including the coronoid and condyloid processes and the angle, is not preserved.

The alveolus suggests that  $P_4$  was longer than  $M_1$ . The molars, which increase in size from  $M_1$  to  $M_3$ , have occlusal surfaces with well-developed main crests and numerous lesser crenulations and also are surrounded lingually by an elevated cingulum of enamel. They are distinctly more lophate than cusate.



Table 1.—Measurements (in mm) of *Pondaung anomalurids* (all NMMP-KU numbers).

	<i>P. anomaluropsis</i>		<i>?P. anomaluropsis</i>		anomalurid sp. 1		anomalurid sp. 2			
	0213 (holotype)		0049		0047		0231		1533	
	a-p	tr	a-p	tr	a-p	tr	a-p	tr	a-p	tr
M <sub>1</sub>	2.6	2.2	—	—	—	—	ca. 2.3	2.1	2.2	2.0
M <sub>2</sub>	2.7	2.5	2.8	2.5	2.8	2.8	2.3	2.2	—	—
M <sub>3</sub>	3.2	2.6	3.1	2.2	—	—	2.5	2.2	—	—

The first lower molar is worn heavily enough to have some of the pattern on the trigonid obliterated. Still prominent features of the occlusal surface are as follows: a strong anterolophid between protoconid and metaconid; an ectolophid extending obliquely posterolingually from protoconid to the intersection of hypoconid and hypolophid; a mesolophid that has complex subdivisions lingually; a hypoconid that is canted anterobuccally; a long, straight hypolophid; and a strong, posteriorly convex posterolophid that, with the hypolophid, encloses a transversely elongate valley.

The less worn M<sub>2</sub> preserves more detail of the pentalophodont occlusal surface. Antero- and posterolophid, ectolophid, and hypoconid-hypolophid resemble those on M<sub>1</sub>. In addition, M<sub>2</sub> preserves the metalophulid I, which is complex lingually—appearing to bifurcate and have a short posteriorly extending process. The mesolophid appears to be double at the ectolophid junction, and its more posterior extension is bifurcate lingually.

The last lower molar, the largest of the three, is similarly complex. It differs from M<sub>2</sub> mainly in having a posterolophid that protrudes more posteriorly. The posterolingual part of the posterolophid is broken from the specimen, so its full extent is not determinable.

Probably also referable to *P. anomaluropsis* is NMMP-KU 0049, a left mandibular fragment with M<sub>2-3</sub> so badly eroded that very little pattern remains. Traces of multiple lophids suggest that this is an anomalurid, and its size (Table 1) puts it near *Pondaungimys*. It is from Wka or Kdw locality (Mogaung area, Fig. 1; Tsubamoto et al., 2000, fig. 7, pl. 1 I; the specimen was collected by local villagers, so the exact locality is not certain).

Anomalurid sp. 1

NMMP-KU 0047 (Fig. 3A), a left M<sub>2</sub>, has a somewhat similar but more complex occlusal pattern than that of *Pondaungimys*, and the tooth is larger and relatively wider transversely than those of *Pondaungimys*. Because the sample size of Pondaung rodents is too small to provide any indication of individual variation, this specimen is tentatively considered to represent another anomalurid taxon. It is from Wka or Kdw locality (Mogaung area, Fig. 1; Tsubamoto et al., 2000, fig. 7, pl. 1 G).

Anomalurid sp. 2

NMMP-KU 1533 (Fig. 4A), a right mandibular fragment with M<sub>1</sub> and alveoli for the other cheek teeth (Pk1 locality, Bahin area), and NMMP-KU 0231 (Pk2 locality, Bahin area; Fig. 1; Tsubamoto et al., 2000, fig. 5, pl. 1 D–F), a right mandibular fragment with M<sub>1</sub>–M<sub>3</sub> (Fig. 4B), represent a smaller species. Both specimens have more worn teeth than NMMP-KU 0213 of *Pondaungimys*. The remaining pattern and basic pentalophodont structure indicate that this is an anomalurid, probably close to *Pondaungimys* if not the same genus. The mandible of NMMP-KU 1533 has a deep masseteric fossa and strong ventral ridge as in *Pondaungimys*.

Anomalurid sp.

NMMP-KU 0048 (Fig. 3B), a right maxillary fragment with P<sup>3-4</sup>, has the size and morphology that suggest reference to *Pondaungimys anomaluropsis*. The anterior root of the zygoma occurs in line with P<sup>3</sup> to the middle of P<sup>4</sup>, and juts out at a greater angle than in a similarly sized *Sciuravus*, suggesting that there may have been an enlarged infraorbital

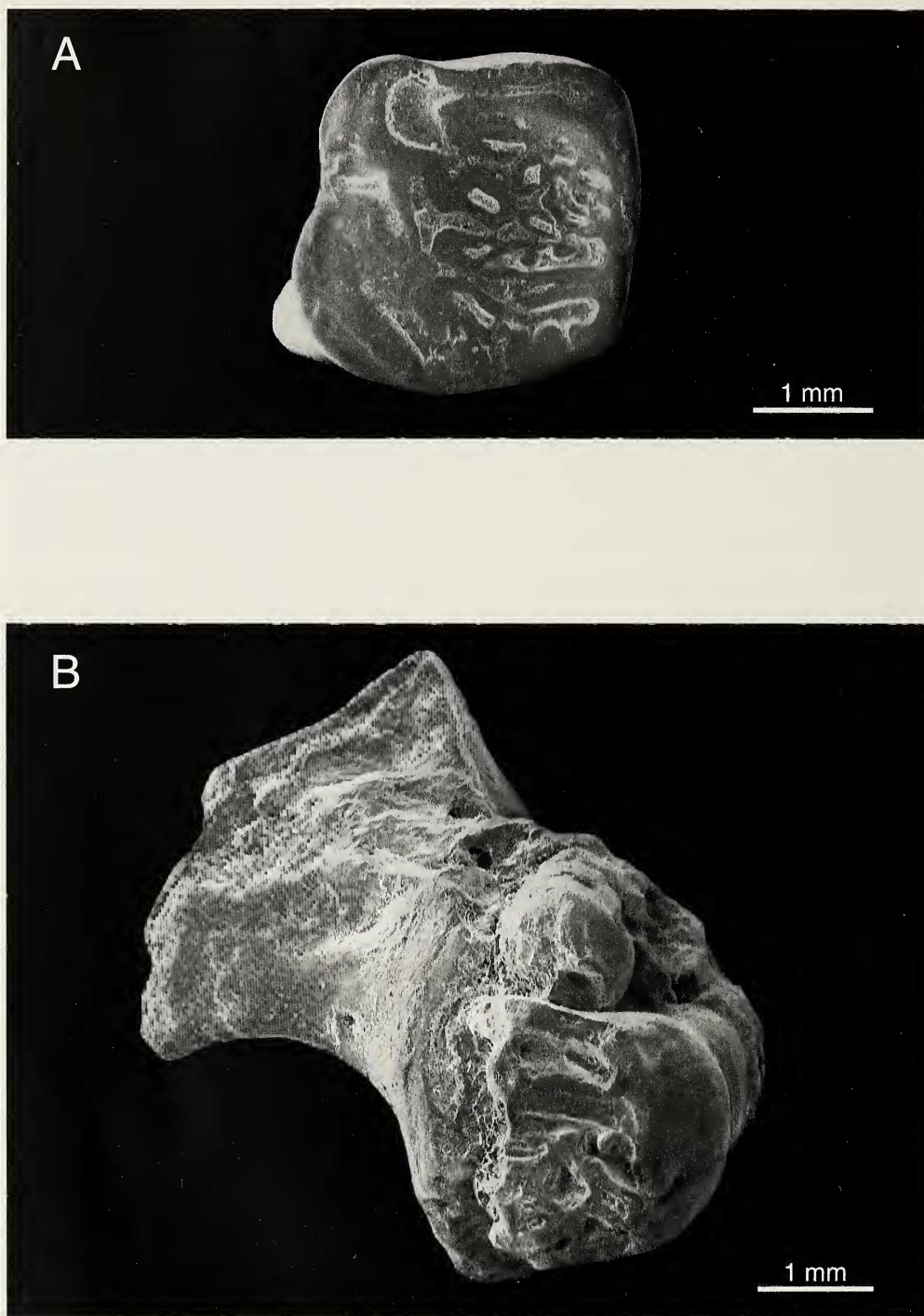


Fig. 3.—A. *Anomalurid* sp. 1, NMMP-KU 0047, occlusal view of left  $M_2$ . B. *Anomalurid* sp., NMMP-KU 0048, occlusal view of maxillary fragment with  $P_{3-4}$ .

foramen as in modern anomalurids.  $P^3$  is a simple peg (anteroposterior, 0.9 mm; transverse, 1.1 mm). This tooth is absent in Miocene and later members of the family.  $P^4$ , broken buccally, preserves a strong cingulum around the remaining sides (anteroposterior, 2.4 mm). It has a distinct protoloph, long mesoloph that bifurcates lingually, sending one arm to the metaloph, and a complete metaloph. The hypocone is set off by a small lingual notch, but as is the case with the lower molars, the tooth is basically more lophate than cusate. NMMP-KU 0048 is from Wka or Kdw locality (Mogaung area, Fig. 1; Tsubamoto et al., 2000, fig. 7, pl. 1H).

## DISCUSSION

Although the family Anomaluridae has been listed as a component of several Paleogene faunas (Krabi, Thailand; Taqah, Oman; Bugti, Pakistan), the only previously described Eocene anomalurid is *Nementchamys lavocati* from the ?late Eocene Bir El Ater or Nementcha locality of the Nementcha Mountains of Eastern Algeria (Jaeger et al., 1985). A taxon based on isolated upper and lower teeth, *Nementchamys* has distinctly anomalurid features in its basically pentalophodont lower molars, complete lingual wall of the lower molars and buccal wall of the upper molars, and the somewhat concave occlusal surfaces of the cheek teeth. *Pondaungimys* and *Nementchamys* clearly share many dental characters, although the latter is more derived in complexity of accessory crests.

The origin of the Anomaluridae was traced to the late early or early middle Eocene Zegdoumyidae (Vianey-Liaud et al., 1994; Vianey-Liaud and Jaeger, 1996), which are known from Glib Zegdou (Algeria) and Chambi (Tunisia). Three genera have been recognized, *Zegdoumys*, *Glibia*, and *Glibemys*, based on twenty-nine isolated teeth. These genera, which exhibit a variety of dental morphologies, have different degrees of similarity to anomalurids. This is shown especially in early stages of pentalophodonty, multiplication of accessory crests, and some development of a lingual wall on the lower cheek teeth. Of them, *Glibia pentalopha* is most similar to *Pondaungimys* in development of transverse lophs, and *Glibemys algeriensis* is most similar in morphology of the lingual wall of the lower molars. However, *Pondaungimys* is more derived than any of the Zegdoumyidae in having the characteristic anomalurid features of a complete lingual wall of the lower cheek teeth and more distinct pentalophodonty. On the other hand, the zegdoumyids are more derived than *Pondaungimys* and other anomalurids in absence of a complete ectolophid in the lower molars (Vianey-Liaud et al., 1994), a character shared with the Gliridae (Hartenberger, 1971) as well as with some Sciuravidae (Korth, 1984).

Morphological and biogeographic considerations led Vianey-Liaud and Jaeger (1996) to hypothesize an ancestral position of the Zegdoumyidae to both the graphiurine Gliridae (elevated by them to family Graphiuridae) and the Anomaluridae. The first postulate, relationships between Zegdoumyidae and graphiurines, is supported by their dental morphology. However, the suggestion of affinities between the zegdoumyids and the anomalurids is less well supported by known fossils. The very strong ectolophid and complete lingual wall on the lower cheek teeth in both the oldest-known anomalurids, *Pondaungimys* and *Nementchamys*, for example, are marked differences from zegdoumyids, *Graphiurus*, and other glirids.

A more complete fossil record would help in determining relationship among these families, but for the Gliridae, including *Graphiurus*, and Anomaluridae, molecular evidence from living forms provides some additional evidence. For example, the Gliridae have been shown to group with the Sciuroidea, based on an analysis of the combined data from three genes, whereas the Anomaluridae group with a "mouse-related clade" that includes Castoridae, Geomyoidea, and Myodonta (Huchon et al., 2002). A study of the GHR gene shows, further, that *Graphiurus* groups as do the other glirids with the sciurid-aplodontid





Fig. 4.—Anomalurid sp. 2. A. NMMP-KU 1533, occlusal view of right mandibular fragment with  $M_1$  and alveoli for the other cheek teeth. B. NMMP-KU 0231, occlusal view of right mandibular fragment with  $M_1$ – $M_3$ .

clade (Waddell and Shelley, in press). Although the source of the anomalurids is still not clear, molecular evidence does suggest a separate origin for anomalurids and glirids. The role of the zegdoumyids in this scheme is here interpreted to involve, on the basis of an admittedly incomplete fossil record, close relationships to glirids but not to anomalurids.

Biogeographic considerations show that glirids are known to have inhabited southern France by the end of the early Eocene, Paleogene Mammal Level MP 10 (Escarguel, 1999). Thus, the fossil record could support the concept of a migration by glirids from southern Europe into Africa and origin there of the zegdoumyids. No glirids are known from Asia until the latest Oligocene, precluding such a source for the zegdoumyids. As for the anomalurids, presence of *Pondaungimys* in southeast Asia opens the possibility of phylogenetic connections with several groups of non-ctenodactyloid Asian rodents, but whether with ischyromyids or others remains a matter of speculation.

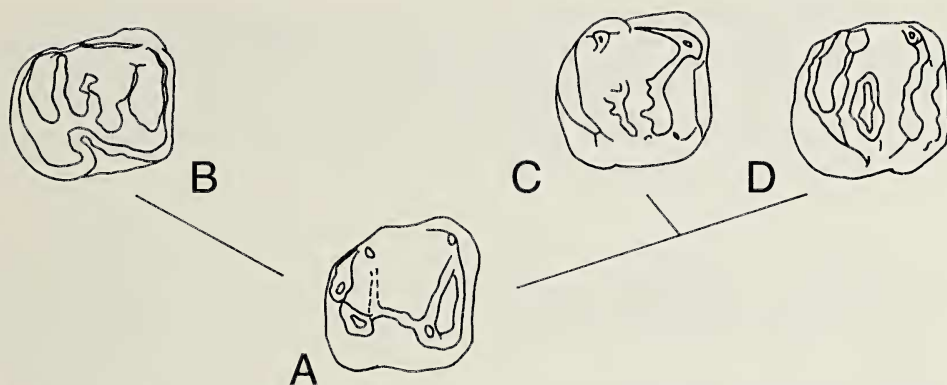


Fig. 5.—Occlusal surfaces of lower  $M_{1or2}$  of an ischyromyid, an anomalurid, a glirid, and a zegdumyid, comparing the primitive condition having a complete ectolophid (A, *Eoischyromys* from the middle Eocene of China, and B, *Pondaungimys*) with the derived reduction or absence of it (C, *Gliravus robiacensis* of MP 16 of France, and D, *Glibia pentalopha*). After: A, Wang et al., 1998; B, This paper; C, Hartenberger, 1971; and D, Vianey-Liaud et al., 1994.

*Pondaungimys* is the oldest anomalurid currently recognized, as well as the oldest indication of the family in Asia. Suggestion of some diversity within the family in the Pondaung localities may imply a still earlier record in southeast Asia, allowing time for diversification in the wet coastal area represented by the fluvio-deltaic depositional setting of the upper part of the Pondaung Formation (Aung et al., 2002). The occurrence of anomalurids in the Pondaung fauna and in the younger Krabi locality of Thailand and in the Nementcha locality of Algeria is another indication of faunal exchange between Africa and southeastern Asia in the middle to late Eocene, documented also among other rodents, Primates and Artiodactyla (Chaimanee et al., 1997; Ducrocq et al., 1997; Marivaux et al., 2000). The dispersal of these rodents probably occurred by the end of the middle Eocene, but neither the precise route nor the environmental conditions for the faunal exchange are known. Lack of any trace of anomalurids in the known fossil record of central Asia seems to indicate that the migration took place south of the Tethys Sea.

The Neogene record of anomalurids can be traced to *Paranomalurus* and *Zenkerella* from the early Miocene of Kenya. Dentally these genera are very similar to extant anomalurids, and an ulnar fragment suggests that the gliding locomotion used by *Anomalurus* and *Idiurus* had developed by that time (Lavocat, 1973).

Both *Pondaungimys* and *Nementchamys* have dental patterns that are more complex than in Miocene and later anomalurids, in which five or fewer transverse lophs provide the only pattern on the cheek teeth. Recent anomalurids feed on sap, bark, flowers, leaves, fruit, and insects (Julliot et al., 1998). The complexity of crests in the occlusal pattern of the cheek teeth in Eocene anomalurids suggests different feeding habits, but the functional significance of complex folds on rodent molariform teeth, present also in such Eocene rodents as *Thisbemys*, *Lophiparamys*, and *Eutypomys*, is not yet clear.

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Recent specimens of anomalurids for comparative work. Mark Klingler prepared the illustrations. Thanks are also due to Professor Nobuo Shigehara (Primate Research Institute, Kyoto University) for his financial support and encouragement for this work, and to Drs. Yukimitsu Tomida (National Science Museum, Japan) and Patricia A. Holroyd (University of California) for their help in collecting literature. This research was supported by the Overseas Scientific Research Funds (No. 14405019 to N. Shigehara) and the 21st Century COE Program of Kyoto University (Leader, T. Nishida) from the Ministry of Education, Culture, Sports, Science and Technology of Japan.

#### LITERATURE CITED

- AUNG NAING SOE. 1999. Sedimentary facies of the upper part of the Pondaung Formation (in central Myanmar) bearing late middle Eocene anthropoid primates. Pp. 152–178, in *Proceedings of the Pondaung Fossil Expedition Team* (Pondaung Fossil Expedition Team, eds.). Office of Strategic Studies, Ministry of Defence, Yangon.
- AUNG NAING SOE, MYITTA, SOE THURA TUN, AYE KO AUNG, TIN THEIN, B. MARANDAT, S. DUCROCQ, AND J.-J. JAEGER. 2002. Sedimentary facies of the late middle Eocene Pondaung Formation (central Myanmar) and the paleoenvironments of its Anthropoid Primates. *Comptes Rendus Palevol*, 1:153–160.
- AYE KO AUNG. 1999. Revision on the stratigraphy and age of the primate-bearing Pondaung Formation. Pp. 131–151, in *Proceedings of the Pondaung Fossil Expedition Team* (Pondaung Fossil Expedition Team, eds.). Office of Strategic Studies, Ministry of Defence, Yangon.
- . 2001. The primate-bearing Pondaung Formation in the upland area, north-west of central Myanmar. Pp. 10–11, in *Abstracts of Anthropoid Origins Symposium* (Powdermill Nature Reserve, April 20–21, 2001).
- BENDER, F. 1983. *Geology of Burma*. Gebrüder Borntraeger, Berlin.
- CHAIMANEE, Y., J.-J. JAEGER, V. SUTEETHORN, AND S. DUCROCQ. 1997. A new late Eocene anthropoid primate from Thailand. *Nature*, 385:429–431.
- COLBERT, E. H. 1937. A new primate from the upper Eocene Pondaung Formation of Burma. *American Museum Novitates*, 951:1–18.
- . 1938. Fossil mammals from Burma in the American Museum of Natural History. *Bulletin of the American Museum of Natural History*, 74:255–436.
- COTTER, G. DE P. 1914. Some newly discovered coal-seams near the Yaw River, Pakokku district, Upper Burma. *Records of the Geological Survey of India*, 44:163–185.
- DUCROCQ, S., AUNG NAING SOE, AYE KO AUNG, M. BENAMMI, BO BO, Y. CHAIMANEE, THAN TUN, TIN THEIN, AND J.-J. JAEGER. 2000. New anthracotheriid artiodactyl from Myanmar, and the relative ages of the Eocene anthropoid primate-bearing localities of Thailand (Krabi) and Myanmar (Pondaung). *Journal of Vertebrate Paleontology*, 20(4):755–760.
- DUCROCQ, S., Y. CHAIMANEE, V. SUTEETHORN, S. TRIAMWICHANON, AND J.-J. JAEGER. 1997. The age of the Krabi mammal locality (South Thailand). Pp. 177–182, in *Actes du CongesBiochroM'97* (J.-P. Aguilar, S. Legendre, and J. Michaux, eds.). Mémoires et Travaux Ecole Pratique des Hautes Etudes 21.
- EAMES, F. E. 1951. A contribution to the study of the Eocene in western Pakistan and western India: D. Discussion of the faunas of certain standard sections, and their bearing on the classification and correlation of the Eocene in western Pakistan and western India. *Quarterly Journal of the Geological Society of London*, 107:173–200.
- ESCARGUEL, G. 1999. Les rongeurs de l'Eocene inferieur et moyel d'Europe occidentale. *Palaeovertebrata*, 28(2–4):89–351.
- HARTENBERGER, J.-L. 1971. Contribution a l'étude des genres *Gliravus* et *Microparamys* (Rodentia) de l'Éocène d'Europe. *Palaeovertebrata*, 4(4):97–135.
- HOLROYD, P. A., AND R. L. CIOCHON. 1994. Relative ages of Eocene primate-bearing deposits of Asia. Pp. 123–141, in *Anthropoid Origins* (J. G. Fleagle and R. F. Kay, eds.). Plenum Press, New York.
- . 1995. A new artiodactyl (Mammalia) from the Eocene Pondaung Sandstones, Burma. *Annals of Carnegie Museum*, 64:177–183.
- HUCHON, D., O. MADSEN, M. J. J. B. SIBBALD, K. AMENT, M. J. STANHOPE, F. CATZEFELIS, W. W. DE JONG, AND E. J. P. DOUZERY. 2002. Rodent phylogeny and a timescale for the evolution of Glires: evidence from an extensive taxon sampling using three nuclear genes. *Molecular Biology and Evolution*, 19(7):1053–1065.
- JAEGER, J.-J., C. DENYS, AND B. COIFFAIT. 1985. New Phiomorpha and Anomaluridae from the late Eocene of north-west Africa: phylogenetic implications. Pp. 567–588, in *Evolutionary Relationships among Rodents: a multidisciplinary analysis* (W. P. Luckett and J.-L. Hartenberger, eds.). Plenum Press.
- JULLIOT, C., S. CAJANI, AND A. GAUTIER-HION. 1998. Anomalures (Rodentia, Anomaluridae) in Central Gabon: species composition, population densities and ecology. *Mammalia*, 62:9–21.
- KORTH, W. W. 1984. Earliest Tertiary evolution and radiation of rodents in North America. *Bulletin of Carnegie Museum of Natural History*, 24:1–71.



- LAVOCAT, R. 1973. Les Rongeurs du Miocène d'Afrique orientale. 1. Miocène inférieur. Mémoires et Travaux Ecole Pratique des Hautes Etudes, 1:1–284.
- MARIVAUX, L., M. BENAMMI, S. DUCROCQ, J.-J. JAEGER, AND Y. CHAIMANEE. 2000. A new baluchimyine rodent from the late Eocene of the Krabi Basin (Thailand): palaeobiogeographic and biochronologic implications. *Comptes Rendus de l'Académie de Sciences, Paris*, 33:427–433.
- PILGRIM, G. E. 1925. The Perissodactyla of the Eocene of Burma. *Palaeontologia Indica*, n.s. 8, 3:1–28.
- . 1927. A *Sivapithecus* palate and other primate fossils from India. *Palaeontologia Indica*, n.s., 14:1–26.
- . 1928. The Artiodactyla of the Eocene of Burma. *Palaeontologia Indica*, n.s., 13:1–39.
- PILGRIM, G. E., AND G. DE P. COTTER. 1916. Some newly discovered Eocene mammals from Burma. *Records of the Geological Survey of India*, 47:42–77.
- STAMP, L. D. 1922. An outline of the Tertiary geology of Burma. *Geological Magazine*, 59(11):481–501.
- THOMAS, H., J. ROGER, S. SEN, M. PICKFORD, E. GHEERBRANT, Z. AL-SULAIMANI, AND S. AL-BUSAIDI. 1999. Oligocene and Miocene terrestrial vertebrates in the southern Arabian Peninsula (Sultanate of Oman) and their geodynamic and palaeogeographic settings. Pp. 430–442, in *Fossil vertebrates of Arabia* (P. J. Whybrow and A. Hill, eds.). Yale University Press, New Haven.
- TSUBAMOTO, T., N. EGI, M. TAKAI, N. SHIGEHARA, AYE KO AUNG, TIN THEIN, AUNG NAING SOE, AND SOE THURA TUN. 2000. A preliminary report on the Eocene mammals of the Pondaung fauna, Myanmar. *Asian Paleoprimateology*, 1:29–101.
- TSUBAMOTO, T., M. TAKAI, N. SHIGEHARA, N. EGI, SOE THURA TUN, AYE KO AUNG, MAUNG MAUNG, T. DANHARA, AND H. SUZUKI. 2002. Fission-track zircon age of the Eocene Pondaung Formation, Myanmar. *Journal of Human Evolution*, 42(4):361–369.
- VIANEY-LIAUD, M., AND J.-J. JAEGER. 1996. A new hypothesis for the origin of African Anomaluridae and Graphiuridae (Rodentia). *Palaeovertebrata*, 25(2–4):349–358.
- VIANEY-LIAUD, M., J.-J. JAEGER, J.-L. HARTENBERGER, AND M. MAHBOUBI. 1994. Les rongeurs de l'Eocène d'Afrique nord-occidentale [Glib Zegdou (Algérie) et Chambi (Tunisie)] et l'origine des Anomaluridae. *Palaeovertebrata*, 23(1–4):93–118.
- WADDELL, P. J., AND S. SHELLEY. In press. Evaluating placental inter-ordinal phylogenies with novel sequences including RAG1,  $\gamma$ -fibrinogen, ND6 and MT-TRNA and MCMC driven nucleotide, amino acid and codon models. *Molecular Phylogenetics and Evolution*.
- WANG, B., R. ZHAI, AND M. R. DAWSON. 1998. Discovery of Ischyromyinae (Rodentia, Mammalia) from the Middle Eocene of North China. *Vertebrata Palasiatica*, 36(1):1–12 (in Chinese, English summary).
- WELCOMME, J.-L., M. BENAMMI, J.-Y. CROCHET, L. MARIVAUX, G. METAIS, P.-O. ANTOINE, AND I. BALOCH. 2001. Himalayan forelands: palaeontological evidence for Oligocene detrital deposits in the Bugti Hills (Balochistan, Pakistan). *Geological Magazine*, 138(3):397–405.